Journal of Experimental Botany, Vol. 60, No. 1, pp. 99–105, 2009
doi:10.1093/jxb/ern272 Advance Access publication 26 November, 2008

Journal of Experimental Botany
www.jxb.oxfordjournals.org

RESEARCH PAPER

CO_2 efflux, CO_2 concentration and photosynthetic refixation in stems of *Eucalyptus globulus* (Labill.)

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Received 19 May 2008; Revised 14 September 2008; Accepted 8 October 2008

Abstract

In spite of the importance of respiration in forest carbon budgets, the mechanisms by which physiological factors control stem respiration are unclear. An experiment was set up in a *Eucalyptus globulus* plantation in central Portugal with monoculture stands of 5-year-old and 10-year-old trees. CO_2 efflux from stems under shaded and unshaded conditions, as well as the concentration of CO_2 dissolved in sap [CO_2^*], stem temperature, and sap flow were measured with the objective of improving our understanding of the factors controlling CO_2 release from stems of *E. globulus*. CO_2 efflux was consistently higher in 5-year-old, compared with 10-year-old, stems, averaging 3.4 versus 1.3 μmol m^{-2} s^{-1}, respectively. Temperature and [CO_2^*] both had important, and similar, influences on the rate of CO_2 efflux from the stems, but neither explained the difference in the magnitude of CO_2 efflux between trees of different age and size. No relationship was found between efflux and sap flow, and efflux was independent of tree volume, suggesting the presence of substantial barriers to the diffusion of CO_2 from the xylem to the atmosphere in this species. The rate of corticular photosynthesis was the same in trees of both ages and only reduced CO_2 efflux by 7%, probably due to the low irradiance at the stem surface below the canopy. The younger trees were growing at a much faster rate than the older trees. The difference between CO_2 efflux from the younger and older stems appears to have resulted from a difference in growth respiration rather than a difference in the rate of diffusion of xylem-transported CO_2.

Key words: *Eucalyptus globulus*, refixation, stem respiration.

Introduction

Respiration represents a major flux of carbon between the biosphere and the atmosphere (Cernusak *et al.*, 2006). In forests, autotrophic respiration consumes about half of the carbon fixed by photosynthesis (Waring *et al.*, 1998). Tree stems and branches contribute from 20–50% of the total amount of CO_2 released by autotrophic respiration (Cernusak *et al.*, 2006; Damesin *et al.*, 2002; Maier *et al.*, 2004). However, despite its importance, the physiological and environmental factors controlling stem CO_2 efflux to the atmosphere are still poorly understood (Teskey *et al.*, 2008).

In this study, the causes of different rates of CO_2 efflux from tree stems of two ages and sizes of the same species are addressed. Several studies reported wide variation in stem CO_2 efflux in stems and branches of different sizes under similar environmental conditions (Cernusak and Marshall, 2000; Damesin *et al.*, 2002; Sprugel, 1990). These differences may be explained by the proportion of living cells in the tissues (Levy and Jarvis, 1998). In above-ground woody tissues, most live cells are found in the periderm, phloem, and vascular cambium. Some live cells are also found in rays of the xylem

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sapwood. In many species the proportion of ray cells and the thickness of the vascular cambium decreases as stem size increases (Ceschia *et al.*, 2002) which could result in lower CO_2 efflux from larger stems. Another possible explanation is that the CO_2 dissolved into xylem sap and transported upward may diffuse into the atmosphere more readily from smaller diameter woody tissues.

In some instances, it has been shown that 40–70% of the CO_2 diffusing out of the stem originated from respiring cells lower in the stem and roots (Teskey and McGuire, 2007). The amount of transported CO_2 depends on several factors including sap velocity, temperature, pH, and anatomical barriers to diffusion (Teskey *et al.*, 2008). Sap velocity can be particularly important in influencing the rate of CO_2 diffusion from stems because it affects the xylem CO_2 concentration [CO_2] (Teskey and McGuire, 2002). In studies of field-grown *Populus deltoides* (Bartr. ex Marsh.) and *Quercus alba* (L.) trees, when sap velocity decreased, stem [CO_2] and CO_2 efflux both increased (Saveyn *et al.*, 2008; Teskey and McGuire, 2002).

Corticular photosynthesis is another process that may change the rate of CO_2 efflux in different sized stems. Trees frequently have chlorophyll beneath the bark surface (Pearson and Lawrence, 1958; Pfanz *et al.*, 2001, 2002). Corticular photosynthesis refixes CO_2 that was released by woody tissue respiration and is likely to differ in stems and branches of different diameters and bark thicknesses.

This study took place in two *Eucalyptus globulus* (Labill.) plantations of two different ages. With few exceptions (Ryan *et al.*, 2004; Cernusak *et al.*, 2006) CO_2 efflux from woody tissues of *Eucalyptus* trees has not been reported, so the role of stem CO_2 efflux in the carbon balance of *Eucalyptus* forests is largely unknown.

The objective of this study was to improve our understanding of the factors controlling CO_2 efflux from stems in *Eucalyptus* trees of different sizes by analysing the relationships between stem CO_2 efflux, CO_2 concentration in the xylem, sap flow and xylem temperature; and by quantifying the importance of CO_2 refixation in the stem under ambient light conditions.

Materials and methods

Study site

The experiment was conducted in central Portugal, in two monoculture stands of *Eucalyptus globulus* (Labill.) belonging to the same clone. One stand was 5-years-old (5y) and the other was 10-years-old (10y). The distance between the stands is about 35 km (38°22′ N 8°19′ W and 38°35′ N 8°36′ W for the 5y and 10y stands, respectively). Tree spacing was 3.5×2 m in the 5y stand and 3×2 m in the 10y stand. A plot of similar area was established in each stand. Average diameter at breast height was 8.9 and 10.4 cm, respectively, for 5y and 10y trees. Diameter increase was measured by dendrometer bands previously installed on the trees.

Climatic conditions were very similar in the two stands. Average air temperature, vapour pressure deficit, and total solar radiation were obtained from a meteorological station (www.snirh.pt) located close to the two stands (38°39′ N 8°15′ W). Soil moisture content was measured with a soil profile probe (PR1, Delta-T, Cambridge, UK) through an access tube located in the centre of each plot. Soil nitrogen and phosphorus contents were estimated using resin capsules (PST-1, UNIBEST, Bozeman, Montana, USA). At each plot, eight capsules were buried in the soil at two different depths (15 cm and 30 cm) for 85 d and removed at the end of the experiment (23 October). Nutrient extraction and analysis followed the method described by Skogley and Doberman (1996). Meteorological and soil data recorded during the experiment in the two plots are shown in Table 1.

Measurements

Measurements were made on four randomly chosen 5y and six randomly chosen 10y trees. Measurements were made on 9 and 10 October 2007 on the 5y trees and 16–17 of the same month on the 10y trees. CO_2 efflux from the stems was measured with an infrared analyser (IRGA) (LI-6400, Li-Cor, Lincoln, NE, USA) in open configuration. A standard conifer chamber was adapted to perform stem measurements by replacing the acrylic cuvette with a clear acetate sheet that was fixed to the stem with adhesive foam bands approximately 1.5 m above the ground. The acetate sheet covered approximately 50% of the circumference of the stem and was approximately 160 mm tall. Measurements were repeated three times per day (morning, midday, and afternoon), first under ambient light conditions and then after shading the chamber with insulated foil. During each efflux measurement, photosynthetically active radiation (*PAR*) reaching the stem surface was also determined under ambient light and shaded conditions with a light meter (LI-170, Li-Cor, Lincoln, NE, USA), placed parallel to the stem surface, at three positions around the cuvette: above, east, and west. The average of *PAR* measured above and at both sides of the cuvette ranged from 15–840 μmol m^{-2} s^{-1}. Shading resulted in an average decrease in *PAR* of about 80%. The CO_2 concentration of the

Table 1. Average daily air temperature, vapour pressure deficit (*VPD*), total radiation, soil moisture, nitrogen and phosphorus in 5-year-old (5y) and 10-year-old (10y) *Eucalyptus globulus* in October 2007

Standard errors of the average are shown in brackets (N=8 for soil N and P and N=12 for soil moisture).

	5y	10y
Temperature (°C)	20.3	20.3
VPD (kPa)	18.24	17.44
Total radiation (MJ m^{-2} d^{-1})	15.8	12.8
Soil moisture: 60 cm depth (% vol)	12.8 (±1.04)	11.3 (±0.08)
Soil moisture 100 cm depth (% vol)	27.1 (±3.17)	37.2 (±1.45)
Soil N (g m^{-2})	0.19 (±0.04)	0.11 (±0.03)
Soil P (g m^{-2})	0.03 (±0.006)	0.04 (±0.008)

air supplied to the IRGA chamber was fixed at 380 μmol mol^{-1}. Shading did not result in changes in cuvette temperature. Relative humidity in the cuvette was kept constant for each measurement under light and shade conditions.

CO_2 concentration in the xylem sap was measured simultaneously with CO_2 efflux measurements. Xylem [CO_2] was measured with solid state non-dispersive infrared (NDIR) CO_2 sensors (GMM222, Vaisala, Woburn, MA, USA) inserted into the stem above the cuvette by drilling a hole about 50 mm into the tree, inserting the sensor, and sealing it at the tree surface with rubber sealant (Qubitac, Qubit Systems, Kingston, Ontario, Canada). Cores previously collected in the same plots showed, by infiltration with a saphranin solution, that the trees had no heartwood, and hence sensors were in contact only with the xylem. Following McGuire and Teskey (2002) and Teskey and McGuire (2007), gas phase [CO_2] measured by the sensor was converted to include the concentration of all dissolved products of CO_2 in the sap ([CO_2^*]) by applying Henry's Law. For these calculations, stem temperature and pH of xylem sap were required. Xylem temperature was measured with thermocouples inserted into the stem near the sensors. Xylem pH was measured in sap expressed from 5 mm diameter cores extracted from each tree with an increment borer. The core was compressed with a vice until the sap was released. In some trees, sap could not be obtained from the core, so, instead, xylem sap was expressed from twigs with a pressure chamber (Model 1000, PMS, Corvallis, Oregon, USA). Twig measurements of pH were corrected to stem xylem pH by a linear regression developed between core and twig measurements from other trees. Expressed sap from the cores and twigs was collected with a Pasteur pipette and transferred to a solid state pH microsensor connected to a pH meter (Red-Line Standard Sensor, Argus Meter; Sentron Europe, Roden, NL). All pH measurements were performed once per day at the same time before beginning the efflux measurements, or the day before, as previous experiments demonstrated that daily variations in sap pH are not significant (A Saveyn, personal communication). The pH of the sap expressed from cores averaged 3.97 for 5y and 3.85 for 10y trees. Over the course of measurements xylem [CO_2] ranged from 3.8% to 13%, which corresponded to [CO_2^*] ranging from 1.8 mmol l^{-1} to 4.3 mmol l^{-1}.

Sap flux density was measured according to the method described by Granier (1985, 1987). Sensors consisted of two probes inserted in the stem 10 cm apart, one above the other. Both probes measured temperature with copper-constantan thermocouples, while only the upper probe was continuously heated. Sap flux density was calculated by the temperature difference between the two probes (Granier, 1985, 1987). Measurements were recorded every 3 min with a data logger (CR10X, Campbell Scientific, Logan, UT, USA and DL2, Delta-T, Cambridge, UK) and averaged every 30 min. Sensor depth was 13 mm for 5y trees and 20 mm for 10y trees. Sap flow (l h^{-1}) was calculated as the product of sap flux density and sapwood area. Sapwood was considered equal to the whole xylem cross-sectional area as cores demonstrated that trees had no heartwood.

Data analysis

Q_{10} was calculated by fitting efflux data to an exponential model (Ryan, 1991):

$$\mathrm{CO_2\ efflux} = \mathrm{CO_2\ efflux_0} \times e^{(\mathrm{kT})} \quad (1)$$

where T is temperature (°C), k (°C^{-1}) is the temperature coefficient, and CO_2 $efflux_0$ is the CO_2 efflux at 0 °C. Q_{10} is the proportional increase in respiration with a 10 °C increase in temperature and is given by $e^{(k10)}$.

The effect of stem size on efflux was tested following the equation proposed by Levy and Jarvis (1998). According to these authors the influence of size on CO_2 efflux from woody organs can be determined by the relationship between the rate of CO_2 efflux expressed on a surface area (S) or volume (V) basis and the ratio of surface area to volume (S/V). When efflux is not affected by stem size, it will be more strongly related to surface area than to volume. In that case, a positive linear relationship should be observed between CO_2 efflux per unit volume and the reciprocal of the stem diameter according to the logic:

$$\text{If } \mathrm{CO_2\ efflux} \propto S, \text{ then } \mathrm{CO_2\ efflux}/V \propto S/V \quad (2)$$

and

$$S/V = \frac{2\pi rl}{\pi r^2 l} = \frac{2}{r} \quad (3)$$

Thus,

$$\mathrm{CO_2\ efflux/V} \propto d^{-1} \quad (4)$$

Statistical differences between trees of different ages were assessed by t test. Linear and multiple linear regressions were applied to investigate the relationships between variables, and slopes of regressions were tested for differences by comparing their confidence intervals. Conditions of normal distribution and homoscedasticity were always tested and variables transformed when necessary. All tests were performed using SPSS (version 15.0, SPSS, Chicago, Illinois, USA).

Results

Site average CO_2 efflux, xylem [CO_2^*], sap flow, and growth rate

Average daily CO_2 efflux (Fig. 1A) and xylem [CO_2^*] (Fig. 1B) were significantly lower (t test, P <0.001) in the 10y compared with the 5y trees. However, the differences in efflux and xylem [CO_2^*] between ages were not proportional. Efflux was 60% lower in the 10y compared with the 5y stems, while [CO_2^*] was only 20% lower. On the other hand, sap flow tended to be higher in the 10-year-old trees (Fig.1C), but differences between the means were not statistically significant (t test, P=0.082), probably as a consequence of the large variability among trees at each site. The rate of diameter growth was substantially lower in the

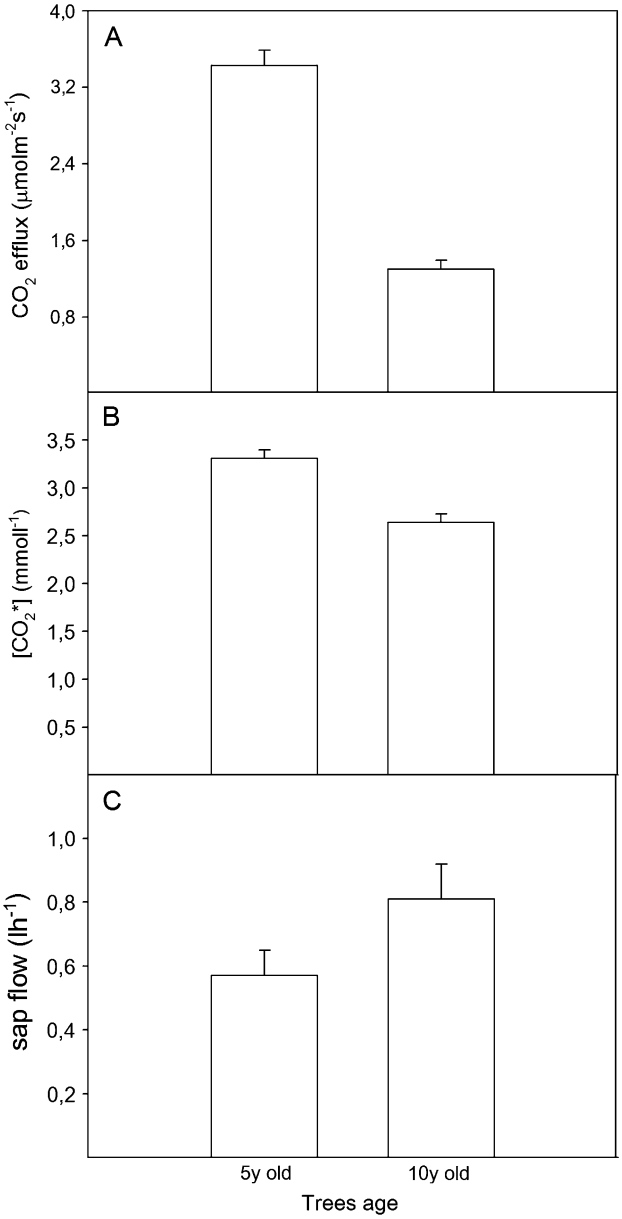

Fig. 1. Daily averages of CO_2 efflux (A), CO_2 concentration in the sapwood ([CO_2^*]) (B), and sap flow (C) in 5-year-old (5y) and 10-year-old (10y) *Eucalyptus globulus* measured in October 2007. Each point is the average of all site measurements. Vertical bars represent standard errors (N=27–36).

10y trees, averaging 0.14 mm d^{-1}, compared with 0.46 mm d^{-1} in the 5y trees.

Corticular photosynthesis

Each efflux measurement was repeated in ambient light and after shading the stem, which reduced incident PAR by 80%. The relationship between measurements under light and shade conditions was found to be the same for both 5y and 10y trees in spite of different rates of CO_2 efflux and even though measurements were taken at different times of the day (morning, midday, and afternoon) and at different ambient light intensities (Fig. 2). The slope of the regression

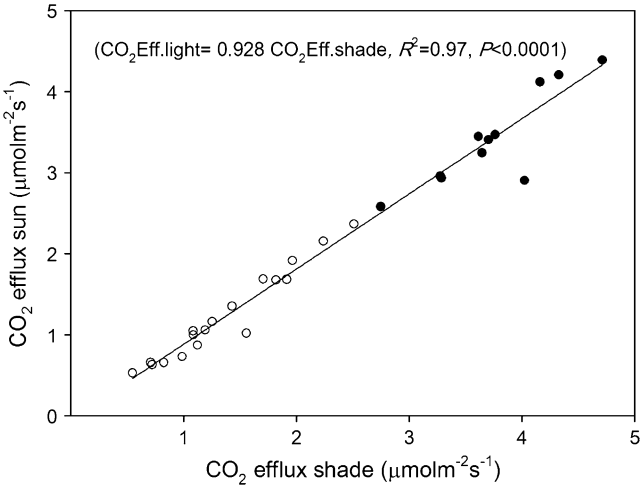

Fig. 2. Relationship between stem CO_2 efflux in 5-year-old (closed symbols) and 10-year-old (open symbols) *Eucalyptus globulus* trees measured in light (*y*-axis) and shade (*x*-axis) in October 2007. Each point represents one measurement.

line showed a decrease in efflux of about 7% under light conditions, indicating a constant 7% rate of CO_2 refixation by cells beneath the bark across a range of CO_2 efflux in the dark of 0.5–4.7 μmol m^{-2} s^{-1}.

Which variables affect CO_2 efflux from the stem?

Efflux on an area basis was linearly correlated with both stem temperature (T) (Fig. 3, upper panel) and [CO_2^*] (Fig. 3, lower panel). For both variables, linear regressions were fitted separately for the 5y trees (CO_2 efflux=0.12T+0.43, P <0.001, R^2=0.34; CO_2 efflux=0.77 [CO_2^*]+1.09, P <0.001, R^2=0.32.) and the 10y trees (CO_2 efflux=0.08T–0.46, P <0.0001, R^2=0.39; CO_2 efflux=0.66 [CO_2^*]–0.42, P <0.0001, R^2=0.32). For each variable, the slopes of the regression lines were not significantly different between the 5y and 10y trees, suggesting that there was no site or age effect on relationships between efflux, temperature, and [CO_2^*]. However, there was a substantial overall difference in CO_2 efflux between the two age groups, with 5y trees having about 2.5 times greater CO_2 efflux than the 10y trees. This difference could not be explained by either temperature or [CO_2^*].

No correlation was found for efflux or [CO_2^*] with sap velocity or sap flux density. In combination, [CO_2^*] and stem temperature were significantly correlated with CO_2 efflux, together explaining 64% and 76% of the variation in efflux in the 5y and 10y trees (Table 2). Sap flux was also included in the model but it was non- significant.

Q_{10}, calculated by fitting a curve to measured data only for overlapping temperature ranges at the two sites, was 1.82 and 2.64 in 5y and 10y trees, respectively.

Is there a size effect?

Following Levy and Jarvis (1998), the effect of stem size on efflux was tested by analysing the relationship of the daily integral of efflux calculated on a volume basis with the

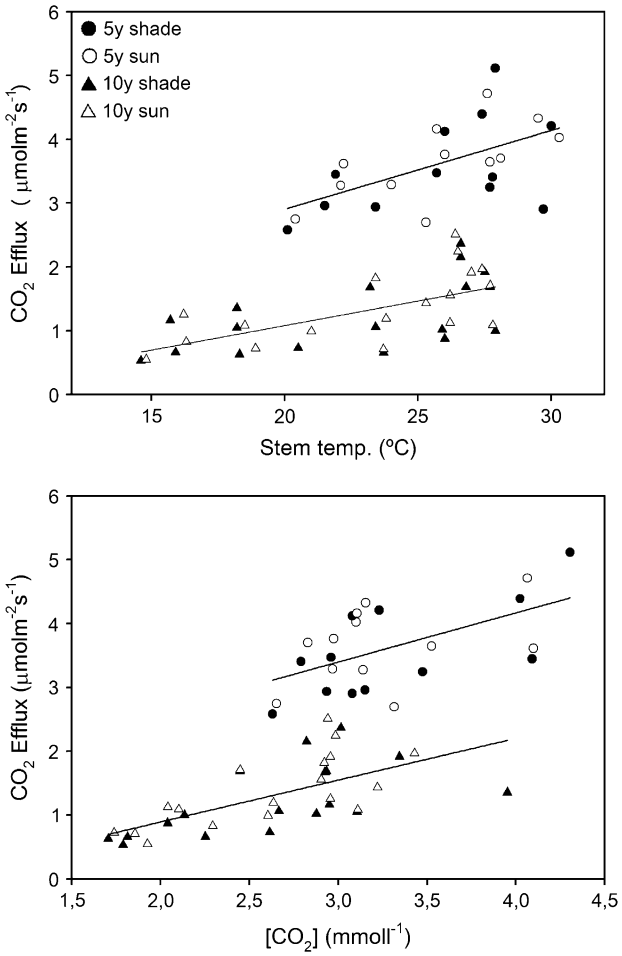

Fig. 3. Relationship between stem CO_2 efflux and stem temperature (upper panel) and stem CO_2 efflux and xylem $[CO_2^*]$ (lower panel) in 5-year-old (5y) and 10-year-old (10y) *Eucalyptus globulus* measured in light and shade in October 2007. Each point represents one measurement.

Table 2. Significance and coefficients of multiple linear regressions of the effect of xylem $[CO_2^*]$ and stem temperature (T) on stem CO_2 efflux in 5-year-old (5y) and 10-year-old (10y) *Eucalyptus globulus* trees in October 2007

(ln CO_2 efflux=b_1+b_2 ln T+b_3 $[CO_2^*]$). P values for each coefficient are shown in brackets.

	5y	10y
R^2	0.64	0.76
P	<0.001	<0.001
b_1	–2.77 (0.003)	–4.50 (0.000)
b_2	0.78 (0.006)	1.97 (0.000)
b_3	1.04 (0.001)	1.09 (0.000)

inverse of tree diameter at breast height (dbh^{-1}) (Fig. 4). If efflux was proportional to stem volume, then its rate calculated on a volume basis should be independent from stem size. A positive linear relationship was found between the daily CO_2 efflux and dbh^{-1}. This indicates that within the range of diameter considered in this experiment (8–13 cm),

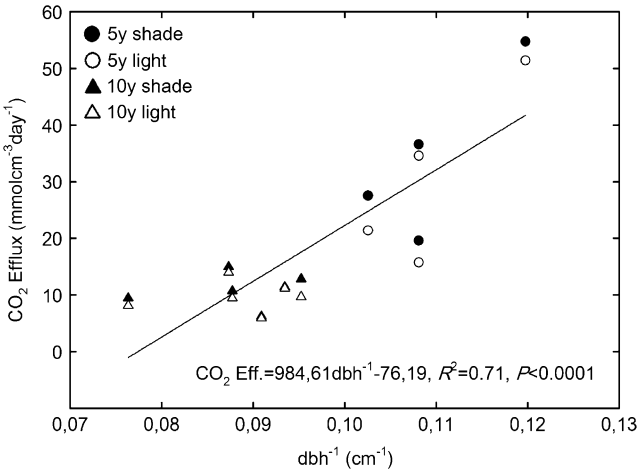

Fig. 4. Relationship between the daily integral of stem CO_2 efflux per tree expressed on a volume basis and the inverse of stem diameter measured at the breast height (dbh^{-1}) in 5-year-old (5y) and 10-year-old (10y) *Eucalyptus globulus* measured in light and shade in October 2007.

the rate of CO_2 efflux was not proportional to stem volume, which is an indication that most of the CO_2 efflux originated near the stem surface.

Discussion

Efflux, temperature, $[CO_2^*]$, and sap flow

Large differences in the magnitude of CO_2 efflux were observed between 5y and 10y trees when compared at similar temperatures and $[CO_2^*]$. In both the 5y and 10y trees CO_2 efflux was correlated with temperature and stem $[CO_2^*]$ in the same way, as indicated by the same slopes of the linear regressions relationships. However, neither temperature nor xylem $[CO_2^*]$ could explain the difference in the magnitude of the efflux between the 5y and 10y trees. The most likely explanation for the difference was the much higher growth rate in the 5y trees with correspondingly higher growth respiration. Since growth respiration is known to be independent of temperature (Ryan, 1991), a difference in growth respiration would explain the offset in the relationships of efflux and $[CO_2^*]$ to temperature between the two ages.

In many tree species including *Liquidambar styraciflua* (L.), *Platanus occidentalis* (L.), *Populus deltoides,* and *Quercus alba,* there has been a positive linear relationship observed between xylem $[CO_2^*]$ and CO_2 efflux which has been interpreted to mean that CO_2 efflux is a combination of the metabolic activity of cells close to the point of measurement and CO_2 that diffuses to the atmosphere from the xylem sap (Teskey *et al.*, 2008). The CO_2 in xylem sap is produced by the metabolic activity of cells lower in the stem and roots and transported upward. Hence $[CO_2^*]$ and sap flow can be important factors for determining the amount of CO_2 released by stems. In this experiment, both age groups had a positive linear relationship between efflux and

[CO_2^*], indicating that the flux of CO_2 out of the stem was dependent on both the CO_2 diffusion gradient between the sapwood and the air and temperature. Together, these factors explained 64–76% of the variation in CO_2 efflux, whereas alone, neither factor explained more than 39% of the variation in efflux.

The linear relationship between efflux expressed on a volume basis and the inverse of dbh indicated that efflux was closely correlated with surface area and not with stem volume (Levy and Jarvis, 1998). A similar correlation was observed in *Pinus densiflora* (Sieb et Zucc.) stems and branches of different sizes (Kim *et al.*, 2007). This result was interpreted to mean that a large proportion of the cells that contributed to efflux were located in or near the cambium and inner bark, in both large and small trees, and that the effect of [CO_2^*] in the xylem was less important to efflux than the respiration of these cells.

The relationship between efflux and surface area may explain why there was no correlation between efflux and sap flow in this study. Considering the large difference in sapwood area between the small and large trees, the high internal [CO_2^*], the lack of correlation between CO_2 efflux and sap velocity and the relatively low correlation between efflux and [CO_2^*], it is reasonable to suggest that in these *E. globulus* trees significant barriers to diffusion existed between the wood and the inner bark that may have impeded the rapid efflux of xylem-transported CO_2 from these stems. Supporting this hypothesis, it has been reported that *E. globulus* trees show an increase in vessel number and a decrease in vessel size on sites with high water stress, frequent in the Mediterranean region, compared to more moist sites, which could slow radial diffusion of gas and reduce CO_2 efflux (Leal *et al.*, 2004).

A negative relationship between sap flow velocity and stem CO_2 efflux has been repeatedly observed (McGuire *et al.*, 2007; Teskey and McGuire, 2002). McGuire *et al.* (2007) interpreted this relationship to mean that the [CO_2^*] in the xylem was diluted when larger quantities of water were taken up by the roots at high rates of sap flow. In this study, the lack of correspondence between sap flow and efflux may also have resulted from low transpiration rates, which were less than 1 mm d^{-1} and about four times lower than the maximum observed in the species in spring under field conditions (David *et al.*, 1997). However, when sap velocity was artificially decreased, CO_2 efflux did not change in *Pinus taeda* (L.) trees in the field (Maier and Clinton, 2006), suggesting that the relationship between sap flow and stem efflux may depend on the species xylem anatomy and the effect it has on the rate of CO_2 diffusion to the atmosphere. Hence, it cannot be determined whether the lack of relationship between sap flow and [CO_2] efflux found here is a characteristic of the species or a consequence of low sap flow.

The importance of refixation

Our measurements of CO_2 refixation were lower than those reported for other species (Teskey *et al.*, 2008). They are also lower than values reported for *E. miniata* (Cunn. et Schauer.) branches at an irradiance of 1000 μmol m^{-2} s^{-1} (Cernusak *et al.*, 2006). In this experiment, measurements of efflux in the light were measured at natural irradiance, which was relatively low since the stems were shaded by the canopy. The average *PAR* measured at the cuvette ranged between 500 and 900 μmol m^{-2} s^{-1} during the midday measurements, and at other times of the day *PAR* values were lower. However, low irradiance may not explain the low CO_2 refixation rates that were measured because the rate of refixation was consistent diurnally at 7% of CO_2 efflux in both young and older tree stems. In *Populus tremula* (L.) twigs, refixation rates increased from 20% to 80% as *PAR* increased up to ~1000 μmol m^{-2} s^{-1} (Aschan and Pfanz, 2003). Photosynthetically active radiation must cross the bark to reach the light-harvesting complexes of the chloroplasts. The amount of light transmitted through the bark varies between 10% and 50% depending on species and age (Aschan and Pfanz, 2003). In *Eucalyptus nitens* (Deane and Maiden) the amount of light transmitted through the bark was found to be 56% of incident *PAR* (Tausz *et al.*, 2005), suggesting that the amount of light reaching the photosynthetic apparatus in the stems of our trees was low.

A second factor potentially affecting CO_2 refixation could be high internal [CO_2^*]. The role of high [CO_2^*] in corticular photosynthesis is controversial. One hypothesis suggests that high [CO_2^*] can favour corticular and wood photosynthesis by inhibiting photorespiration (Cernusak and Marshall, 2000); on the other hand, high [CO_2^*] was found to reduce photochemical efficiency of photosystem II and inhibit photosynthesis in woody tissue of five different species, probably through the acidification of the protoplasm (Manetas, 2004). Acidification of the protoplasm, whether caused by high internal [CO_2^*] or other unknown factors, seems a plausible explanation for low refixation, since average xylem pH in this study was about 3.9 which is substantially lower than the pH found in the xylem of other species (Teskey *et al.*, 2008).

Conclusions

These results have provided an insight into the mechanisms controlling the efflux of respiratory CO_2 from stems to the atmosphere in *E. globulus* trees. It was observed that the relationships between xylem [CO_2^*] or stem temperature and CO_2 efflux were consistent across different sized trees of the same species, even though the actual rate of efflux was substantially different at a given xylem [CO_2^*] in the 5y and 10y tree stems. This points out the need to comprehensively measure both the internal and external the factors that can affect CO_2 efflux. In this study, temperature, xylem [CO_2^*], and growth rate were important factors influencing efflux, but still did not explain all of the variation in efflux. Although rates of CO_2 refixation and sap flux were not important influences on efflux in this species, it is likely that they are important in other species. In addition, energy demand, carbohydrate availability,

oxygen concentrations, water status, and perhaps other factors may need to be measured before stem respiration can be fully characterized. The CO_2 efflux from these trees was related to stem surface rather than volume, but this is not the case in all tree species. It is suggested that each species may have a unique combination of factors that control rates of stem CO_2 efflux, and that the importance of internally transported CO_2 to CO_2 efflux may depend in large measure on xylem anatomy and stem morphology.

Acknowledgements

This work was co-funded by FEDER and by the Portuguese government (Programa Operacional Ciência e Inovação 2010). Sofia Cerasoli is a post-doc fellow of the Fundação para a Ciencia e Tecnologia (SFRH/BPD/28384/2006). The stay of Robert Teskey and Mary Anne McGuire in Portugal was funded by the Luso-American Foundation, project L-V-504/2006.

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